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Canadian Journal of Fisheries and Aquatic Sciences

DOI:
https://doi.org/10.1139/cjfas-2020-0025

Published: 01/10/2020

Peer reviewed version

The effects of trawling and primary production on size-structured food webs in seabed ecosystems

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Abstract

Understanding how different drivers shape relationships between abundance and body mass (size-spectra) is important for understanding trophic and competitive interactions in food webs, and for predicting the effects of human pressures. Here, we sample seabed communities from small polychaetes (< 0.001g) to large fish (> 1kg) in the Celtic Sea to examine how bottom trawling and primary production affect their size spectra, and to compare these to predictions from a model that couples predator and detritivore communities. Size spectra were not well approximated by linear fits because of truncation of the size spectra of detritivores. Low primary production resulted in lower abundance of benthic fauna. Bottom trawling reduced the abundance of predators and large detritivores, but allowed small detritivores to increase in abundance. These empirical size spectra were partly consistent with predictions from the size spectra model, showing that understanding the structuring of benthic communities requires a consideration of both size and functional group. The findings highlight the need for an ecosystem approach to understanding the effects of exploitation and climate change on marine ecosystems.

Key words: Body size; bottom-up; top-down; bottom trawls; macroecology; size distribution; climate change

Introduction

Marine ecosystems are subject to a range of anthropogenic pressures, many of which are increasing in intensity and occurrence (Lotze et al. 2006; Poloczanska et al. 2013). Two important pressures on marine ecosystems are fishing and changes in primary production due to climate change and eutrophication. High levels of fishing pressure can truncate age and size distributions of target and non-target species, drive shifts in maturation to earlier ages and sizes, and remove large predators, which can cause communities to exhibit steeper size spectrum slopes than those exposed to lower fishing intensities (e.g. Daan et al. 2005; Queirós et al. 2006). Changes in primary production can result from eutrophication and might result from climate change (Behrenfeld et al. 2015; Behrenfeld et al. 2006). High levels of primary production can increase rates of growth and biomass accumulation, raising size spectral intercepts (Jennings and Blanchard 2004; e.g. Macpherson et al. 2002). These drivers rarely operate in isolation, and their interactions can generate unexpected ecological responses (Crain et al. 2008). For example, a recent study found that higher levels of primary production make benthic ecosystems more resilient to bottom trawling impacts (Hiddink et al. 2017), and that the effects of bottom trawling on the trait composition of benthos are greater in areas of high primary production (Howarth et al. 2018b). Hence, there is a need to better understand how marine ecosystems react to multiple drivers (Fu et al. 2018).

The body-size distributions of aquatic communities are governed by fundamental ecological principles. In aquatic ecosystems, most predators are larger than their prey because they are unable to consume organisms larger than themselves (Jennings et al. 2002b; Law et al. 2009). This, in combination with higher population growth rates at the base of food webs and inefficient energy transfer between trophic levels, is why large organisms are much rarer within the aquatic environment than small ones (Sprules et al. 2016). A size spectrum characterises the size distribution of all individuals in an ecosystem according to biomass across size classes. When plotted as a frequency distribution of log abundance vs. log body size, these 'size spectra' typically have negative slopes close to -1 which emerge from the predatory, competitive and feeding interactions within ecosystems (Blanchard et al. 2009). This negative slope is a macro-ecological phenomenon that exhibits remarkable regularity among different types of organisms and habitats (Gómez-Canchong et al. 2013; Macpherson et al. 2002). Various models describe how community size spectra arise from individual-level size-based processes (Blanchard et al. 2017). The simplest of these aggregate all individuals within a single size spectrum regardless of their feeding strategy. However, recent evidence

suggests this is too simplistic, as organisms with different trophic positions (e.g. detritivores and predators) are expected to exhibit different size spectra and different responses to pressures. Theory predicts that when food availability falls with body size (as in most aquatic food webs where larger predators eat smaller prey), the size spectrum slope is steeper than when organisms of different sizes compete for a shared unstructured resource (e.g. autotrophs, herbivores and detritivores; hereafter dubbed 'detritivores') (Blanchard et al. 2009).

Blanchard et al. (2009) constructed a size spectrum model that described the feeding interactions between predators and benthic detritivores. Their simplest models were 'uncoupled' and assumed that neither feeding group affected another. In contrast, 'coupled' models were more complex and assumed that predators fed on a range of smaller-sized prey which included detritivores, while detritivores fed on a non-size-structured food pool of detritus. This model predicted that detritivores have shallower, but truncated (with a steeper slope at larger body sizes), size spectral slopes compared to predators, and that predator slopes steepen in response to fishing pressure. Detritivore truncation started at 1g when coupled with predation and at 100g without coupling due to senescence of detritivores. In contrast, fishing was predicted to release detritivores from their predators, resulting in greater abundances of large detritivores and a shallowing of their size spectral slopes. Even though there is clear evidence that bottom trawling affects benthic invertebrates (Sciberras et al. 2018), there is debate about how important this effect is relative to predation release (van Denderen et al. 2013). The Blanchard et al. (2009) model assumed fishing has no direct effect on predators <10g and no direct effect on detritivores. Hence, fishing could only affect detritivores through competition release. High levels of primary production were predicted to provide more energy to the ecosystem, supporting faster growth rates and larger body sizes in both groups, resulting in higher size spectra intercepts and shallower slopes. Conversely, low levels of primary production provided less energy, reducing the abundance of large body sizes and steepening slopes. To date, no rigorous empirical test of these predictions has been carried out.

To improve our understanding of how multiple drivers and predator-prey interactions shape size spectra and affect food web dynamics we test the prediction of the 'coupled' model in Blanchard et al. (2009) with empirical observations. By sampling benthic predators and

detritivores in the Irish and Celtic Seas and the western English Channel across gradients of bottom trawling pressure and primary production, we test the following hypotheses:

H1: The size spectrum slope of detritivores is shallower than that of predators, because detritivores share a common unstructured food source while predators eat prey smaller than themselves and food availability falls with body size because of energy loss in trophic transfers. The detritivore size spectrum will be truncated at larger sizes (>1 g) because detritivores experience predation pressure (Figure 1A sketches the hypothesis).

H2: Higher levels of primary production will provide more energy to the ecosystem, supporting faster growth rates and larger body sizes in both groups, resulting in higher intercepts and shallower slopes. Low levels of primary production will not provide enough energy to support a full range of sizes, so size spectra in the predator communities will be truncated, with relatively steep slopes (Figure 1B).

H3: Bottom trawling will result in steeper size spectral slopes in predators because larger predators are caught and removed (e.g. Nilssen et al. 1986). This will release detritivores from their predators, resulting in greater abundance of large detritivores and therefore a shallowing of detritivores' size spectral slopes (Figure 1C).

Methods

Here we examine normalized size-spectra. A normalized size spectrum converts the biomasses or abundances to densities by dividing them by the width of the size classes (Blanchard et al. 2017). The intercept and the slope of the size spectrum characterise the total abundance in the community and its rate of decrease with body size. We use the terms 'slope', 'intercept' and 'abundance' to describe patterns in the size spectra in this paper. The 'slope' is the slope of the fit through the data of a particular section of the size spectrum. The 'intercept' is defined here as the point where the size spectrum starts, at $\log_{10}$ body mass = -3.

Sampling

This study analyses a dataset described by Howarth et al. (2018b) and available from (Howarth et al. 2018a). In brief, trawling intensity (quantified as the swept-area-ratio, SAR (y^{-1}), from Vessel Monitoring Systems data) and primary production (PP, mg C m^{-2} yr^{-1}, estimated by the MODIS satellite sensor) for the United Kingdom were divided into four categories (divided at equal intervals on a log scale for trawling intensities, and equal intervals on a natural scale for PP, Table 1). Sampling stations were then chosen in the Irish

Sea, Celtic Sea and western English Channel to cover all combinations of the four levels of trawling intensity and primary production on areas of seabed with similar sediments and depths (sand and muddy sand with moderate shear bed stress between 40 and 100m depth, http://jncc.defra.gov.uk/ukseamap). Twenty stations were sampled in September 2015 and again in April 2016 (Figure 2). A retrospective multivariate analysis of the environmental variables at the sampling stations indicated that the environmental conditions at two stations were dissimilar to the others based on their sediment particle size distribution (with very low and very high mean sediment particle sizes respectively). These were excluded from further analyses (details in Howarth et al. 2018b). Hence, data are missing for the combination of low trawling and moderately high primary production. Three different sampling gears were deployed at each station to ensure a large size range of the benthic community (small invertebrates to demersal fish) was captured. Day grabs primarily sampled infauna and very small epifauna, 2m beam trawls primarily sampled large infauna and epifaunal organisms, and 4m beam trawls primarily sampled larger epifauna and fish. All organisms caught were identified to at least family level (often to species), counted, and wet-weighed.

The scaled abundance and biomass were used to create $\log_{10}$ normalised biomass size spectraby aggregating individual body masses into $\log_{10}$ bins. A normalized size spectrum converts the biomasses to densities by dividing them by the width of the body mass classes (Sprules et al. 2016). Abundance and biomass values for the 2m and 4m beam trawls were scaled to account for differences in sampling area and efficiency compared to the Day grab (for which we assumed 100% of the fauna from 0.1 m^2 was collected) as described in Howarth et al. (2018b). The scaling was based on the assumption that $\log_{10}$ normalised biomass in the body mass categories that overlap between the sampling gears are continuous. Biomasses from the 2m beam trawl were scaled so that the $\log_{10}$ normalised biomass per body mass category in the overlapping body mass categories matched the Day grab $\log_{10}$ normalised biomass per body mass category. Subsequently, biomasses from the 4m beam trawl were scaled so that the $\log_{10}$ normalised biomass per body mass category in the overlapping body mass categories matched the (previously scaled) 2m beam trawl $\log_{10}$ normalised biomass per body mass category. For a more detailed description of these methods see the "Gear calibrations" section and Supplementary Material of Howarth et al. (2018b).

Predators are defined here as animals that obtain most of their food by eating and killing whole living organisms. Detritivores are defined as animals that obtain most of their food from plants or detritus (dead organic material) and the group therefore includes herbivores and detritivores (SM, Table S1 lists all the classification for all taxa encountered). Our definition of detritivores and predators is more refined than that of Blanchard et al. (2009), where all grab-collected animals were defined as detritivores and all trawl-caught animals as predators.

Analysis

Because our hypotheses assume non-linear patterns in size spectra (e.g. truncation), linear models were not considered a suitable approximation, especially because non-linearity makes the range of body sizes over which the slope and intercept are fitted very important . We therefore fitted a Generalized Additive Mixed Model (GAMM) using the *gamm* function in the package *mgcv* in R (Wood 2015) to examine the effects of trawling, primary production and feeding strategy on benthic size spectra. Sampling station was included as a random effect because the measurements for the different size-classes are not independent. The response variable is the $\log_{10}$ normalised biomass per body mass category. We fitted and compared GAMMs to test the different hypotheses (Table 2). Interactions were specified using the *te* function in *mgcv* that produces a full tensor product smooth. To make the interpretation of the results easier, H1 and H2 predictions were plotted using only low fishing effort stations (SAR < 1.4 y^{-1}), while H3 predictions were plotted for intermediate PP stations (550-1000 mg C m^{-2} yr^{-1}).

Because the normalised biomass is $\log_{10}$ transformed, size classes without biota resulted in undefined data, which can result in an underestimation of the steepness of size spectra. To avoid this, the normalised biomass for size classes without biota was replaced by a very small value, calculated as 0.5 times the lowest non-zero value in that size class. A sensitivity analysis showed that the results and conclusion were not affected by the replacement value chosen.

Although the survey design used categorisations of bottom trawling intensity and primary production levels, statistical analyses used them as continuous variables for greater power and more accurate estimation of effects. For ease of plotting, however, the fitted values generated by the statistical models were plotted against $\log_{10}$ size class and plotted between

the categorical levels of fishing pressure and primary production (even though the model fitted them as continuous variables).

Results

Combining samples from three different sampling gears resulted in continuous size spectra with $\log_{10}$ body mass classes spanning 6 orders of magnitude from small worms <1mg to large fish >1kg. The recorded size spectra had some distinct deviations from a straight line, in particular for detritivores, and would have therefore been poorly described by simply estimating their intercepts and slopes from linear fits.

The AIC of the GAMM that used PP, bottom trawling intensity and feeding strategy as explanatory variables was lower than that of models that omitted one or more of these variables (Model 6 in Table 2, R^2 = 0.931, n = 464, Figure S2), indicating that each of these variables increased the explanatory power of the model. This full model is therefore used to infer and plot relationships below.

Detritivores were more abundant than predators at body masses <3g and predators were more abundant than detritivores at sizes >10g (H1, Figure 3, Table 2). The detritivore size spectrum slope became steeper (more negative) at $\log_{10}$ body mass > 0 (1 g), while the slope for predators was more constant, suggesting that predation depresses and truncates the abundance of large detritivores. The size spectrum slope for detritivores is therefore similar to that of predators at small body sizes, and steeper at large body sizes. The AIC of the model including feeding strategy was much lower than a model that did not include it (ΔAIC of model 6 vs. model 5 = 331.4 Table 2).

The size spectral intercepts were higher at higher PP for small detritivores, but detritivore size spectra converged at large body sizes, making the size spectral slopes somewhat steeper at high PP (H2, Figure 3, Table 2). For predators, the size spectra had the lowest intercept at the lowest PP, but there was no clear differentiation between the other levels of PP. No truncation of the predator size spectrum was evident at low PP. The AIC of the model that included PP was lower than a model that did not include it (ΔAIC of model 6 vs. model 3 = 59.4, Table 2).

Bottom trawling effort did not affect predator slopes, but the size spectrum was lower over most of the range of body sizes for predators at higher fishing effort (H3, Figure 4, Table 2). Small detritivores were more abundan, while large detritivores were less abundant, at high trawling effort. The AIC of the model that included trawling effort was lower than a model that did not include it (ΔAIC of model 6 vs. model 4 = 49.2, Table 2).

Discussion

This study investigated the effects of bottom trawling and primary production on the size spectra of temperate seabed communities, over six orders of magnitude of body mass. Ours is one of the first studies to empirically compare size spectra between functional groups (Blanchard et al. 2017; Blanchard et al. 2009; Robinson et al. 2016), and it shows that distinguishing between the two feeding strategies improves our ability to understand how food web dynamics translate into size spectra. Our results show that normalised benthic size spectra are not well approximated by linear fits because of truncation in the size spectra of detritivores.

H1, that the slopes of detritivores size spectra would be shallower than those of predators because detritivores share common food sources while predation is size-structured, was not supported by the results. We discuss possible reasons for this further below. The 2nd part of H1, that the detritivores size spectrum is truncated at large sizes because detritivores experience predation pressure, was supported. The comparison of coupled (where predators eat detritivores) and uncoupled (where they do not) models in Blanchard et al. (2009) showed that the body mass at which the truncation begins is driven by the existence of predation on detritivores, beginning at 1g with predation in coupled models and at 100g in uncoupled models due to senescence of detritivores. Our results based on empirical data show that the truncation starts around 1g, indicating that top-down effects of predation on detritivores strongly affect their size spectra. That predatory feeding strategies can support larger body sizes than detritivory is supported by fundamental ecological theory (Elton 1927; Sheldon and Kerr 1972) and empirical studies (Jennings and Mackinson 2003; Jennings and Blanchard 2004; Jennings et al. 2001), both of which suggest that trophic level generally increases with body size. This is because predators tend to ingest prey smaller than themselves and that large organisms feeding at low trophic levels (e.g. baleen whales) are rare (Blanchard et al. 2017; Cohen et al. 1993). Overall, the coupled model predictions were largely consistent with our empirical data, highlighting the importance of predator-

detritivore coupling in food web dynamics. These results therefore show that an understanding of the structuring of benthic communities requires a consideration of both size and functionality.

Higher levels of primary production should equate to greater quantities of phytoplankton, detritus and other organic matter sinking towards the seafloor (Blanchard et al. 2009). In turn, this should result in greater abundances of detritivores and provide more prey to the predator community, and may be why predator size spectra were higher in areas with higher primary production. Conversely, areas with less available energy should be less able to support large body sizes, making the slopes of size spectra more negative as predicted by models (Blanchard et al. 2009). H2, that high levels of primary production would result in higher size spectral intercepts and shallower slopes by providing more energy to the ecosystem, which should support faster growth rates and larger body sizes, was only partly supported. The intercepts of the size spectra were lower at lower PP for both detritivores and predators, but no shallowing of the slopes was evident. In fact, the slope for detritivores was steeper at high PP. The 2nd part of H2, that the predator size spectrum is truncated at large sizes because at low levels of primary production there is not enough energy to support a full range of sizes, was not supported by the results. These findings suggest that although higher PP can support a higher standing stock of benthic invertebrates, the lack of shallower size spectra slopes shows that it does not result in a faster growth of benthic biota, contrary to expectations (Sprules and Munawar 1986). Our understanding of the strength of competition over resources in soft-sediment benthic invertebrates is very limited (Branch 1984; Wilson 1990), but these results suggest that the increase in standing stock (represented by the higher intercept) has increased competition over resources among the benthos, to a level where the same amount of resources are available per unit benthic biomass as at lower PP.

H3 was that bottom trawling will result in steeper size spectral slopes in predators because they are caught at larger sizes, and that this will release detritivores from predation resulting in greater abundance of large detritivores and therefore a shallowing of their size spectral slopes. Although H3 was not supported by the results, we did find a lowering of the size spectra of predators at higher trawling effort, suggesting that the abundance of all predators regardless of size is reduced by trawling. There was no evidence of release of predation pressure on large detritivores, as these also decreased in abundance with trawling effort.

There was, however, an increase in the abundance of small detritivores, which can be indicative of a decrease in predation or a decrease in competition with large detritivores. The coupled model of Blanchard et al. (2009) predicted that fishing causes strongest declines in large predators, in turn releasing detritivores from predation pressure. The model did not include the direct and well-documented effect of bottom trawling on benthic invertebrates, which removes around 10% of fauna in a trawl pass depending on the gear and habitat (Sciberras et al. 2018), decreasing abundance of long-lived biota by 37% on a typical fishing ground (Hiddink et al. 2019). An obvious reason for the lack of an increase in the abundance of large detritivores is, therefore, that the direct negative effect of bottom trawling is larger than the positive effect of predator release. Smaller detritivores did increase in abundance in response to bottom trawling, and this can be explained by a combination of several factors: a release of predation pressure due to removal of predators by trawling (van Denderen et al. 2013); a release from competition with large detritivores due to removal by trawling; and a higher population growth rate which results in a smaller effect of a similar level of fishing mortality (Hiddink et al. 2019). An increase in abundance of small and short-lived fauna in response to trawling is often assumed in modelling studies (Hiddink et al. 2008; van Denderen et al. 2013), but so far empirical evidence for such an increase has been sparse (Hiddink et al. 2019; Jennings et al. 2002c). The conclusion that predation reduces the abundance of large detritivores (H1) may seem to contradict the conclusion that removing predators through trawling does not result in an increase in the abundance of large detritivores (H3). This is not a contradiction though, as explained above. The direct effect of bottom trawling on detritivores outweighs the indirect effect through removal of their predators.

In summary, this is the first study to compare the size spectra of different functional groups across interacting gradients of trawling pressure and primary production. Our results highlight the importance of predator-detritivore interactions for the dynamics of benthic food webs. Overall, some of our results agree with the coupled model predictions of Blanchard et al. (2009), while some results do not match those predictions. Some of these discrepancies seem to be because the direct effects of trawling on detritivores were not included in the coupled model, and this can easily be modified. The reasons for other differences between the empirical data and model predictions (the lack of slope difference between detritivores and predators of small sizes, and the lack of effect of PP on slopes) are less obvious and more fundamental, as they relate to how the processes of growth and

mortality were modelled by Blanchard et al. (2009). These discrepancies suggest that the use of a shared resource by detritivores, rather than a size-structured resource by predators, does not necessarily result in different size spectral slopes. Mechanisms that could explain such deviations are less efficient feeding by large detritivores compared to smaller ones, or a larger predator/prey body mass ratio than expected for predators (Jennings et al. 2002a). Performing separate analyses for detritivores that are commonly preyed upon and for detritivores that are largely inedible may also provide further insights (van Denderen et al. 2013). The findings highlight the interactive effects different stressors have on marine ecosystems, which need to be understood if an ecosystem approach to managing the effects of exploitation and climate change on marine ecosystems is to be effective.

Data accessibility

Data used in this paper are archived in the British Oceanographic Data Centre under doi:10.5285/674d4224-7cc5-4080-e053-6c86abc0626e (Howarth et al. 2018a).

Acknowledgements

This work was supported by the Natural Environment Research Council and Department for Environment, Food and Rural Affairs [grant number NE/L003279/1, Marine Ecosystems Research Programme]. PJS acknowledges support from Natural Environment Research Council through its National Capability Long-term Single Centre Science Programme, Climate Linked Atlantic Sector Science, grant number NE/R015953/1. We would like to thank Ian Pritchard, Wendy Robertson, Tanya Riley, Maria Giulia Moretti-Bushin, Jack Buckingham, Hannah Hernon, Charlotte Mathews, Claude Eric-Marquet, Craig Robertson, Marija Sciberras, Kathryn Hughes, Sowmiya Shivaji, Tom Perkins, Michael Spence, James Pilkington, Julia Rulent, Anna Canning, Gillian Peacock, Pascal Dubois, Anna Krystali, Nikki Lacey, Federico Ghiazza, Lucy Hawkesworth, Sarah Holmes, Sarah Dashfield, Christine Pascoe Natalie Welden, Marine Cendrier and Camille Govoue-Maurin for their assistance with sampling and laboratory work.

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Tables

Table 1. The range of values that defined the four experimental treatments of trawling intensity and primary productivity sampled in this study, and that were used for plotting intensity levels in Figures 2-4.

Treatment	Trawling intensity, BT, swept area ratio (yr^{-1})	Primary production, PP, (mg C m^{-2} yr^{-1})
1 – Low	$\geq 0 \leq 0.4$	$\geq 0 \leq 550$
2 - Medium low	$> 0.4 \leq 1.4$	$> 550 \leq 775$
3 - Medium high	$> 1.4 \leq 5$	$> 775 \leq 1000$
4 - High	$> 5 \leq 15$	$> 1000 \leq 1500$

Table 2. GAMM outputs for statistical comparison of different models. Response variable = $\log_{10}$ Normalized biomass. PP = primary production: mg C m^{-2} yr^{-1}, BT = bottom trawling: swept-area-ratio, y^{-1}, FS = Feeding strategy: predators PD or detritivores DV. The *te* function in mgcv package in R produces a full tensor product smooth. Comparison of the AIC in the column 'Test of' with model 6 provides a test of the hypothesis in that column. Δ_i is differences in AIC values between each model and the most parsimonious model (model 6). w_i are Akaike weights and represent weight of evidence (out of 1.00) that each model is the best model in the set.

	Model	AIC	Δ_i	w_i	Test of:
1	te($\log_{10}$class)	1054.9	321.6	0	
2	te($\log_{10}$class, by = FS)	786.6	53.2	0	
3	te($\log_{10}$class, BT, by = FS)	766.1	32.8	0	H2
4	te($\log_{10}$class, PP, by = FS)	770.6	37.3	0	H3
5	te($\log_{10}$class, BT, PP)	1053.5	320.1	0	H1
6	te($\log_{10}$class, BT, PP, by = FS)	733.4	0.0	1	

Figures

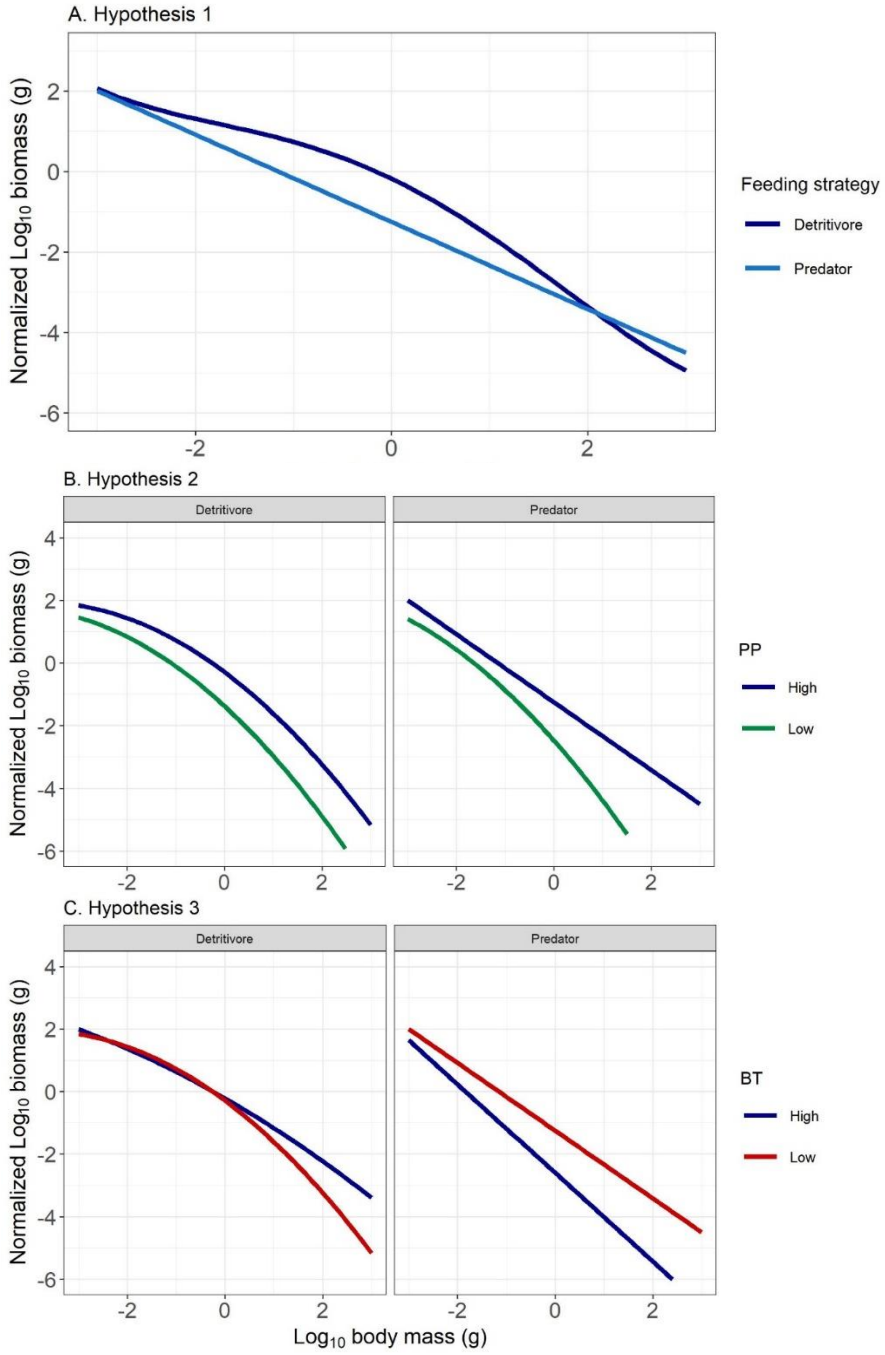

Figure 1. Hypothesized size-spectra for hypotheses 1, 2 and 3. A) Log_{10} normalised size spectra of the benthic community for the two feeding strategies. B) Log_{10} normalised size spectra of the benthic community for the two feeding strategies for different levels of primary production (PP). C) Log_{10} normalised size spectra of the benthic community for the two feeding strategies for different levels of bottom trawling effort (BT).

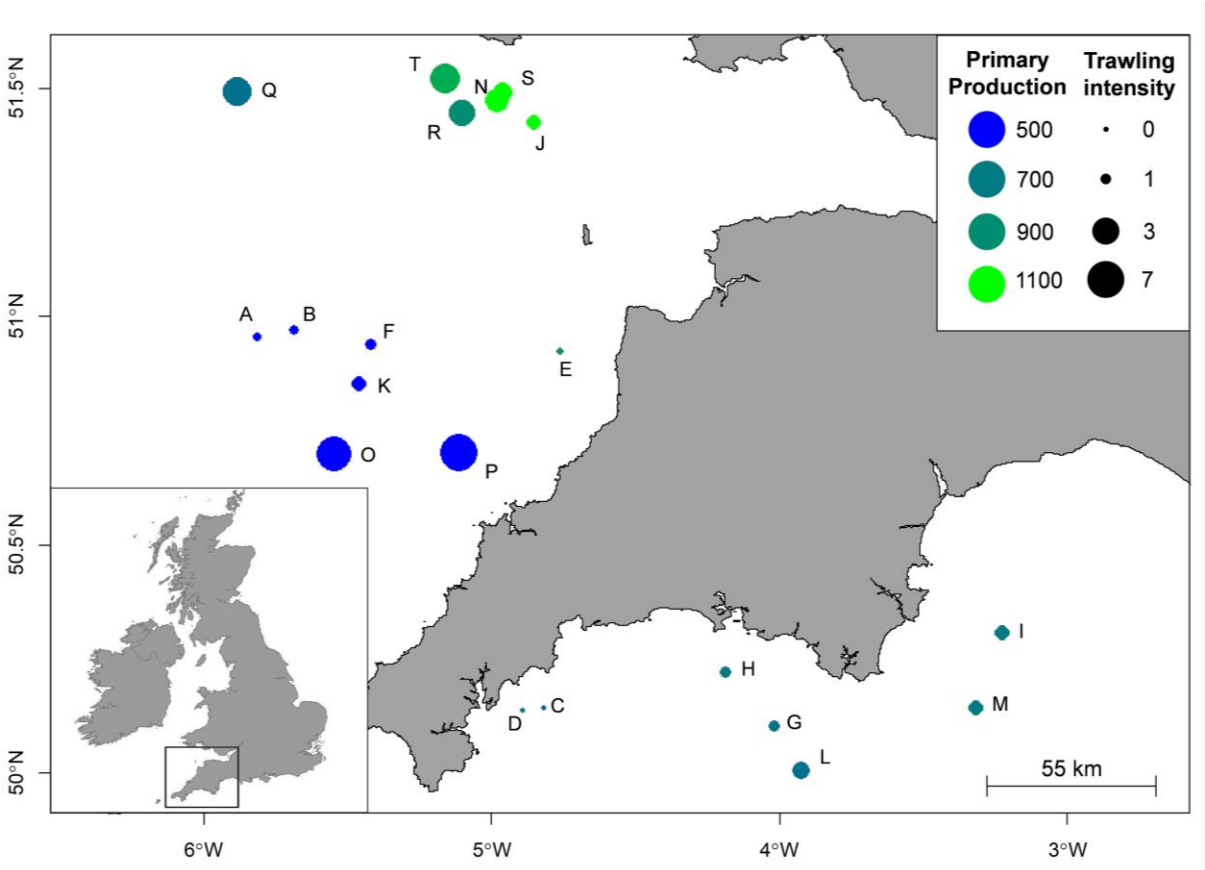

Figure 2. Sampling stations in the study area in southwest of the United Kingdom. Each point represents a 1 x 0.6 nautical mile box, the shade and size of which signifies the level of primary production (mg C m^{-2} yr^{-1}) and trawling intensity (yr^{-1}).

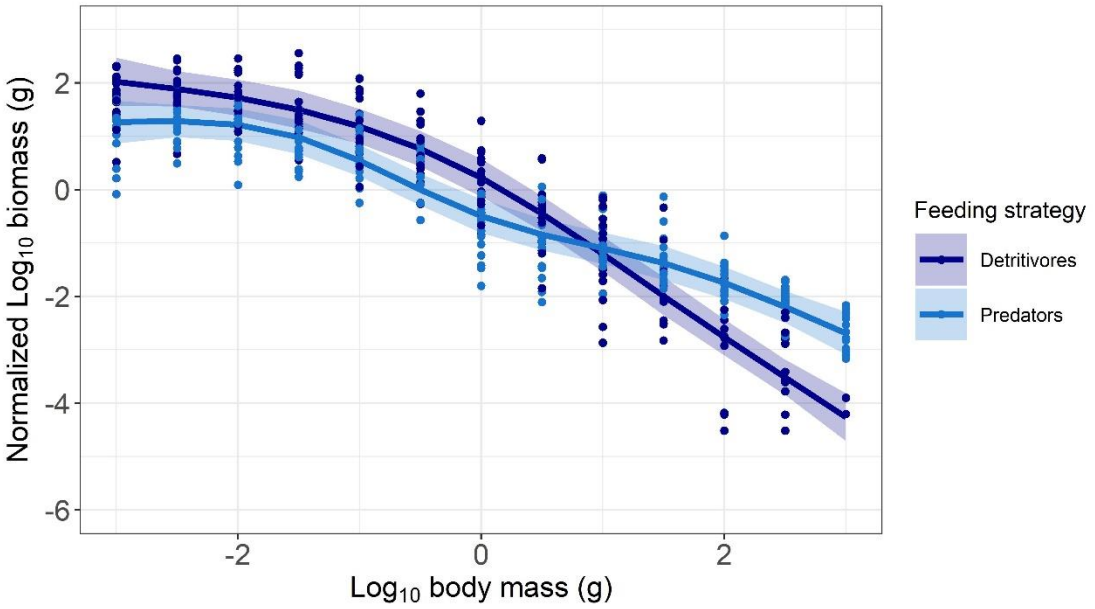

Figure 3. Log_{10} normalised size spectra of the benthic community for the two feeding strategies, for stations with low bottom trawling effort (testing H1). Points show log_{10} normalised biomass per 0.5 m^2 for each size class for each station, and lines and shaded areas represent the fitted GAMM and their 95% confidence intervals.

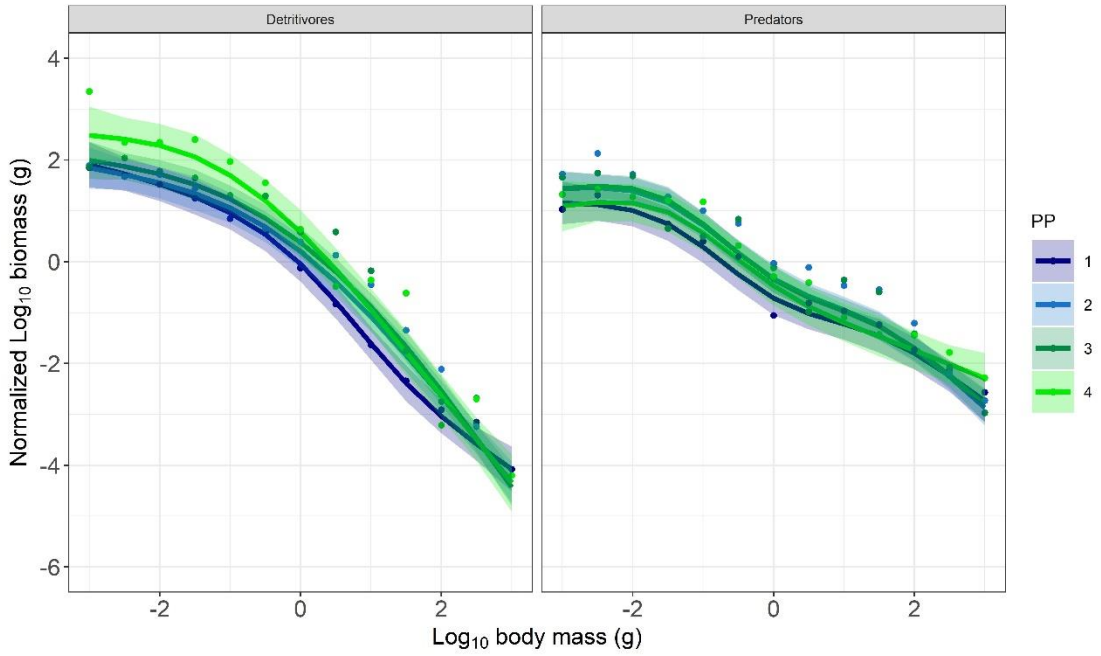

Figure 4. Log_{10} normalised size spectra of the benthic community for the two feeding strategies for different levels of primary production (PP, see Table 1 for category levels), for areas with low bottom trawling effort (testing H2). Points show the mean log_{10} normalised biomass per 0.5 m^2 for each size class over all stations, and lines and shaded areas represent the fitted GAMM and their 95% confidence intervals.

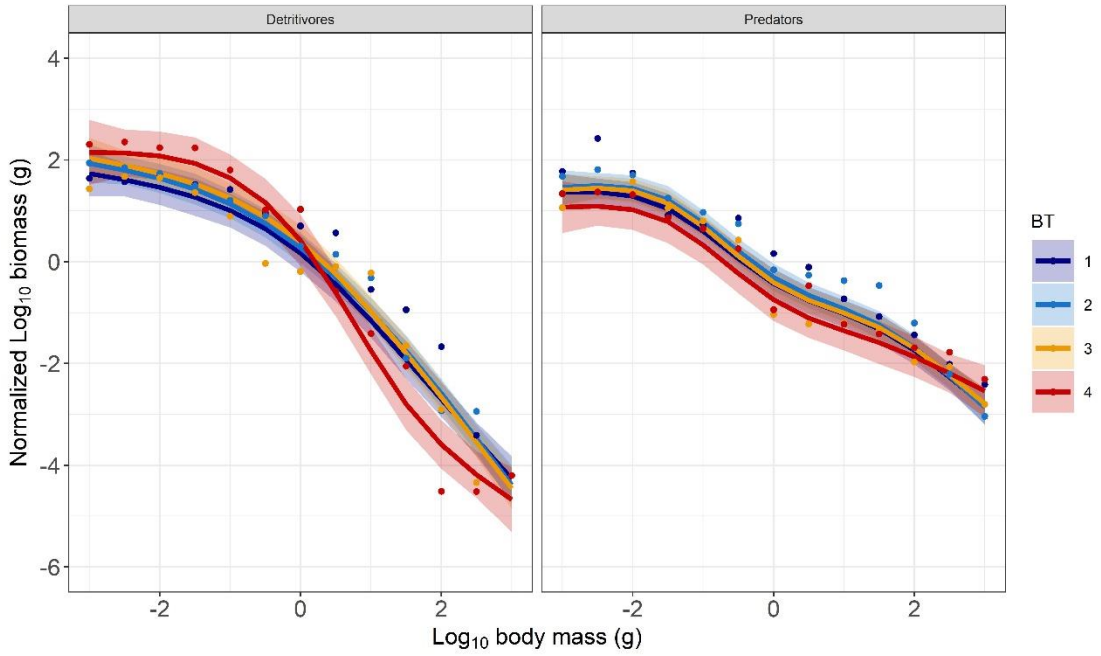

Figure 5. Log_{10} normalised size spectra of the benthic community for the two feeding strategies for different levels of bottom trawling effort (BT, see Table 1 for category levels), for areas with intermediate primary production (testing H3). Points show the mean over all stations log_{10} normalised biomass per 0.5 m^2 for each size class, and lines and shaded areas represent the fitted GAMM and their confidence intervals.